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Perceived segmentation of center from surround by only illusory contours causes chromatic lateral inhibition

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ABSTRACT

When a light and also its surrounding context slowly oscillate in chromaticity over time, the color appearance of the light depends on the relative phase of center and surround. The influence of the surround is generally accounted for by retinotopic center–surround organization, with the surround inhibiting signals from the center. The traditional neural account, however, cannot rule out lateral inhibition due to cortical mechanisms sensitive to object segmentation cues. Experiments here reveal that illusory contours are sufficient to separate a center from its surround. Observers adjusted the Michelson contrast of a matching disk to equal the perceived modulation depth of a central area within a surround. Both the central test and matching disk were maintained at constant luminance and modulated in-phase at 2 Hz along one chromatic axis (L/(L + M) or S/(L + M)). The center was perceptually segmented from the surround by either a physical (retinotopic separation) or illusory (cortically represented) triangle contour. Segmentation of center from surround by the illusory contour strongly attenuated the perceived modulation depth for both chromatic axes. Further, the strength of attenuation was consistently greater with the illusory than the physically segmenting triangle. This cannot be accounted for by retinal center–surround antagonism; instead it points to a cortical neural representation of contours, with lateral inhibition following neural mechanisms sensitive to object segmentation cues.

1. Introduction

Chromatic contrast is a central feature of color appearance. Two separate regions delivering the same spectrum of light to the eye may appear quite different in color depending on the context in which they appear. The change in color appearance due to chromatic contrast classically is attributed to lateral interactions between adjacent stimuli. For example, a small long-wavelength test field appears a less saturated red when presented within a long-wavelength surround, compared to a middle-wavelength surround (Ware & Cowan, 1982). Traditional neural accounts of spatial chromatic contrast concentrate on retinal center–surround spatially antagonistic receptive field organization (Hurvich & Jameson, 1957). An alternative neural account, however, is that perceptual organization, not retinotopic separation, is sufficient to create a center–surround antagonistic relation (D'Antonia & Shevell, 2007). Experiments here reveal that illusory contours can invoke center–surround spatial antagonism to alter color appearance, suggesting a cortical neural locus for lateral inhibition of a center by a surround.

Shifts in color appearance were measured within a central region of a field that slowly oscillated in chromaticity. Chromatic oscillation within a surround will shift the appearance of a central region, whether the central region is steady (D'Antonia & Shevell, 2006; De Valois et al., 1986) or slowly oscillating itself. Analogous measures of the brightness of a central light within a surround that slowly oscillates in luminance show that the center's perceived modulation depth (perceptual peak-to-trough modulation) can either increase or decrease depending on the phase, frequency, and modulation depth of the temporally varying surround (D'Antonia, Kremers, & Shevell, 2011; Kremers & Rimmele, 2007; Kremers et al., 2004). When the surround has the same temporal frequency, phase, and modulation depth as the central field, the perceived modulation depth of the center is attenuated; if the surround phase is opposite to that in the central field, the perceived modulation depth in the center is increased. This is consistent with traditional neural accounts of lateral inhibition in the luminance domain and with physiological properties of center–surround receptive fields in the LGN (Kozyrev, Silveira, & Kremers, 2007; Kremers & Rimmele, 2007; Kremers et al., 2004).

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Previous neural accounts and physiological measures cannot, however, rule out a cortical neural representation of contours where lateral inhibition is generated through mechanisms sensitive to object segmentation cues (D'Antonia & Shevell, 2007). Consider a large circular field slowly oscillating in luminance. When the field is perceptually segmented into central and surrounding regions by adding a thin dark concentric gap, the perceived modulation depth is attenuated in the center, consistent with center–surround spatial antagonism (D'Antonia & Shevell, 2007; Kremers et al., 2004). If, however, that dark gap is varied in perceived stereoscopic depth, but not retinotopic location, the attenuation is eliminated and the center and surround are perceived to be a single temporally-varying field. Finally, if the central area also appears to be moved in depth away from the surround, the attenuation of perceived modulation returns. These findings indicate that retinal center–surround antagonism is *not sufficient* to account for lateral interactions observed for luminance contrast, and suggest a critical role for neural mechanisms sensitive to object segmentation cues.

Equally striking is the attenuation in perceived modulation depth when the center and surround are perceptually segmented by only an illusory contour rather than a dark gap (D'Antonia & Shevell, 2007). The first neural representation of an illusory contour is thought to occur in visual cortical areas beyond V1 (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989; von der Heydt, Peterhans, & Baumgartner, 1984). This result, therefore, suggests that it is *not necessary* for contours to be defined pre-cortically for lateral inhibition to occur. The current study extends these findings to show that perceptual organization also regulates induced temporally-varying percepts of color.

2. Methods

2.1. Observers

Four female observers, ranging in age from 18 to 32, participated in the study. Observers had normal color vision as determined by Rayleigh matching. All observers wore non-tinted eyeglasses or corrective lenses. Observers were paid volunteers naïve to the purpose of the experiment with the exception of author SE. SE has strasbimic amblyopia and therefore wore an eye patch over the left eye, but the others performed the experiment binocularly. All observers completed at least three practice sessions to familiarize themselves with the task before beginning the experiment. The study was approved by an Institutional Review Board at the University of Chicago; written informed consent was obtained for each observer. Results are illustrated and reported for three out of the four observers, as one out of the four observers did not show any significant differences across the experimental conditions.

2.2. Stimuli and procedure

Stimuli were displayed on one of two calibrated color CRTs (NEC Accusync 120 or Sony Triniton) controlled by an Apple iMac computer with internal video capable of digital-to-analog resolution of 10 bits per gun. The software was set to display a resolution of 1280 × 1024 with a 75 Hz non-interlaced refresh rate. A spectroradiometer (PhotoResearch 650) was used to measure the spectral power distribution of the R, G, and B guns. Using a photometer (International Light 1700), the light level of each phosphor was measured throughout its range to find 990 equal steps (0.1% increments) between 1% and 100% of the phosphor's maximum.

Stimuli were specified in an l, s cone-based chromaticity space (MacLeod & Boynton, 1979) modified so the unit of $s = S/(L + M)$ was normalized to 1.0 for equal-energy-spectrum (EES) "white". In this space, the horizontal and vertical axes correspond to relative L- vs. M-cone [$l = L/(L + M)$] and relative S-cone [$s = S/(L + M)$] stimulation, respectively. For each observer, heterochromatic flicker photometry was used to equate phosphor radiances for equiluminant stimuli.

The complete test stimulus was a uniform circular disk 6° in diameter. The disk modulated sinusoidally at 2 Hz along either the l axis (with a fixed value of 0.65 for s) or s axis (with a fixed value of 0.665 for l); luminance was held constant at 10 cd/m^2. The depth of modulation was set to one of four different levels of Michelson contrast for each chromatic direction: 2%, 4%, 6%, or 8% for l; and 10%, 20%, 30% or 40% for s. Observers adjusted the Michelson contrast of a 2° matching disk to match the perceived modulation depth of the central 2° area of the test disk (Fig. 1). The matching and test disks oscillated in-phase at a rate of 2 Hz and were surrounded by a steady uniform field maintained at the average chromaticity ($l = 0.71$, $s = 0.65$ for l axis modulation, and $l = 0.665$, $s = 1$ for s axis modulation). The luminance of the steady uniform field was 9 cd/m^2. The test and matching disk had a small luminance difference compared to the steady field to avoid border melting.

Four experimental conditions were used to vary retinotopic separation vs. perceptual segmentation of the central 2° test area from its surround (6° outer diameter). The conditions were (1) a uniform 6° wide disk alone, used as a baseline condition in which the matched contrast should approach the physical test contrast; (2) as (1) but with an illusory-triangular contour formed by three "pac-men" (each one a 1° diameter disk with a pie-shaped region taken out); (3) as (1) but with a dark luminance gap (0.2° in width) in the shape of a triangle; and (4) the same three "pac-men" used in (2) but rotated 180° to abolish the illusory contour (Fig. 1). The order of testing the four contrasts was randomized within a session for a single axis and condition; each contrast was repeated 5 times within a session. The order of chromatic axis of modulation and condition was randomized within each daily session. Eight runs of 20 trials each were completed in one daily sitting to complete 160 measurements (2 chromatic axes * 4 conditions * 4 contrast levels * 5 replications), and each daily sitting was repeated 3 times. Measurements from each of the five replications were averaged within each session, and daily means were averaged across the

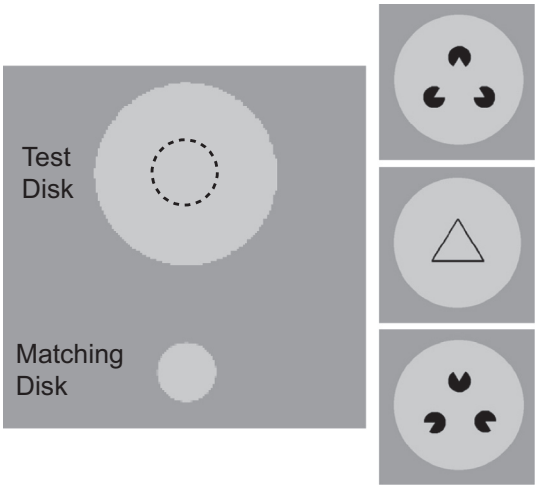

Fig. 1. (Left) The uniform disk experimental configuration. Observers adjusted the modulation depth of the matching disk until it appeared to match the perceived modulation depth within the area of the test disk denoted by the dotted line. The dotted line is added here for clarity and was not physically present in the stimulus. (Right) Illustrations of the three other conditions: the illusory triangle, the physical triangle, and the rotated pac-men.

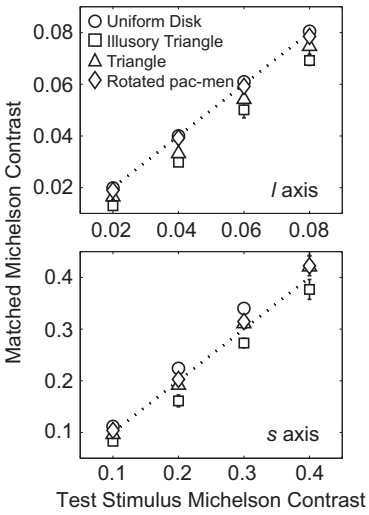

Fig. 2. The perceived modulation depth (vertical axis) as a function of test-stimulus modulation depth along the *l*-axis (top panel) or *s*-axis (bottom panel) for observer NS. Error bars are ±1 SEM from three daily averages (most are smaller than the plotted points so are hidden).

3 days. Standard errors of the mean were calculated using the three daily averages.

2.3. Statistical analysis

For each observer and chromatic axis, an analysis of variance (ANOVA) was performed using fixed factors of test stimulus contrast (4 levels) and experimental condition (4 levels). Fisher–Hayter protected pairwise comparisons were used to compare the perceived temporal modulation depth across the conditions in each ANOVA. Unless otherwise stated, reported statistics refer to protected pairwise comparisons at significance level $p < 0.05$.

3. Results

Fig. 2 shows perceived modulation depth as a function of stimulus contrast along the *l* (top panel) and *s* (bottom panel) axes for one observer. Perceptual segmentation of center from surround clearly altered the strength of perceived chromatic modulation in the center. When the center was segmented from the surround with an illusory triangle (squares), perceived modulation depth was significantly attenuated compared to all other conditions for each chromatic axis.

Fig. 3 (top panel) plots for three observers the ratio of matched contrast in each condition to the matched contrast for the uniform disk (circles in Fig. 2) for *l*-axis modulation. The bottom left panel shows the statistical significance of differences among means across the four conditions, as determined by the Fisher–Hayter protected pairwise comparisons. Fig. 4 is comparable to Fig. 3 but for *s*-axis modulation. The middle and right panels in Figs. 3 and 4 are for two additional observers. These plots show that the perceived modulation was significantly attenuated also for the physical triangular contour compared to the uniform disk for two of the observers. Further, the degree of attenuation cannot be attributed merely to the presence of the pac-men forming the contour. The rotated pac-men condition is identical to the illusory triangle condition with the exception that the pac-men did not align to create an illusory contour. The rotation reduced the attenuation of perceived modulation depth compared to aligned illusory contour pac-men, and, with the exception of one case, never was significantly different from the uniform-disk condition.

Although either retinotopic separation or perceptual segmentation of the center from surround influenced perceived modulation, the strength of attenuation with the illusory triangle was consistently stronger compared to the physical triangle. The consistently stronger attenuation with the illusory contour shows that retinotopic separation of the center from surround is *not necessary* for chromatic lateral inhibition to occur. This result is not consistent with retinal center–surround antagonism, and instead suggests that lateral interactions underlying these induced changes in color appearance are cortical in origin and depend on object segmentation.

3.1. Test of perceived brightness enhancement

The formation of illusory contours is linked to perceived brightness enhancement throughout the illusory area (Jory & Day, 1979; Kanizsa, 1979; Watanabe & Oyama, 1988), an effect that does not

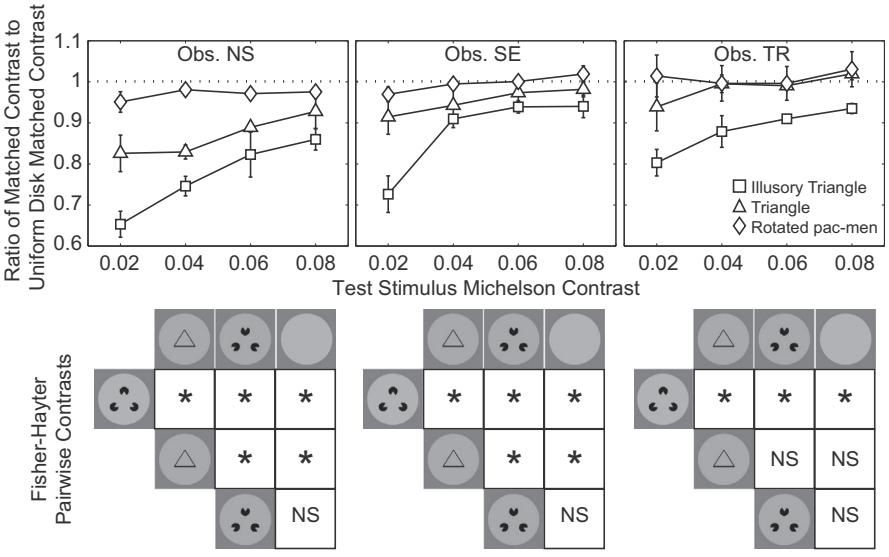

Fig. 3. (Top panels) The ratio of matched contrast to the uniform-disk matched contrast for stimuli oscillating along the *l* axis. Error bars are ±1 SEM from three daily averages. (Bottom panels) Results of Fisher–Hayter protected pairwise comparisons (*$p < 0.05$, NS = not significant) for each of the three observers.

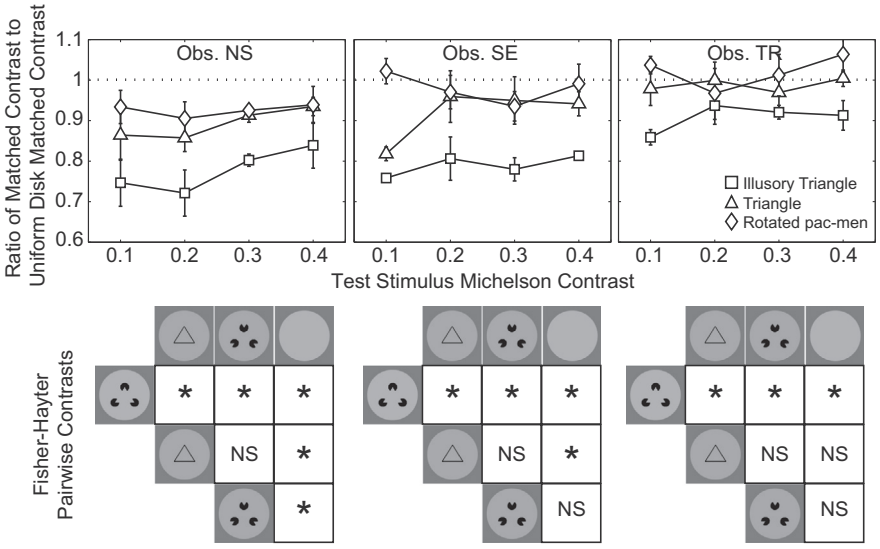

Fig. 4. As Fig. 3 but for stimuli oscillating along the *s* axis.

necessarily occur within areas bounded by physical contours. The perceived brightness increment might have the effect of a broadband increment (e.g., "whiteness") within the illusory area. If so, the perceived saturation of chromatic stimuli would decrease, potentially leading to a reduction in perceived chromatic modulation depth under the current conditions. To test this possibility, two observers repeated the illusory triangle condition with *s*-axis modulation. The pac-men were presented as either a luminance decrement (0 cd/m^2, as before) or increment (*l*, *s* values of 0.665, 1.0, which is metameric to equal-energy-spectrum "white", at luminance 20 cd/m^2), relative to the constant luminance of the test and matching disks at 10 cd/m^2. An ANOVA was performed for each observer with fixed factors of test-stimulus contrast (4 levels) and experimental condition (4 levels). Stronger attenuation with the decremental compared to incremental pac-men was seen for both observers ($p < 0.05$), but perceived modulation was still attenuated with the incremental pac-men compared to the uniform disk ($p < 0.05$) or the physical triangle ($p < 0.05$ for NS, and $p = 0.05$ for SE). This is shown in Fig. 5, which plots the ratio of matched contrast for the physical triangle (from Fig. 4) and the illusory triangle with incremental or decremental pac-men, compared to the previously measured uniform-disk matched contrast. While a perceived increase in brightness within the illusory triangle area formed by the dark pac-men may increase the strength of attenuation, it cannot account fully for the attenuation caused by an illusory contour separating center from surround.

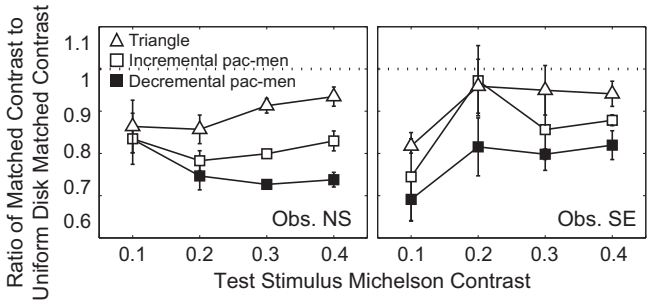

Fig. 5. The ratio of matched contrast to the uniform-disk matched contrast for the physical triangle or the illusory triangle with pac-men defined by a luminance increment (open squares) or decrement (filled squares), for chromatic modulation along the *s* axis. Error bars are ±1 SEM for three daily averages.

3.2. Equiluminant stimuli

These experiments suggest that the illusory contours themselves are critical to the perceived segmentation of center from surround. If true, there should be less attenuation of perceived modulation when the pac-men are equiluminant to the test and matching disk due to the decreased visibility of contours under equiluminant conditions (Gegenfurtner, Brown, & Rieger, 1997; Gregory, 1977; Li & Guo, 1995). Two observers repeated the original four conditions using equiluminant triangular and pac-men stimuli to generate the contours. In this experiment, the triangular contour and pac-men had [*l*, *s*] values of [0.71, 1.4] and a luminance of 10 cd/m^2 (equiluminant to the test and matching disks) for *l*-axis modulation. This created an increment in S-cone stimulation compared to the uniform disk, but maintained average M- and L-cone stimulation. For *s*-axis modulation, [*l*, *s*] values of [0.71, 1] were chosen to increase L-cone stimulation (with a corresponding decrease in M-cone stimulation) but maintained the average S-cone stimulation. Consistent with the prediction, the attenuation of perceived modulation in the center was sharply reduced with equiluminant contours. One observer showed slight but significant ($p < 0.05$) attenuation with modulation along the *l* axis in conditions with retinotopic separation or perceptual segmentation, but the strength of attenuation was much weaker compared to conditions with a luminance difference (Fig. 6, left column). The attenuation was never significant in any condition for the second observer (Fig. 6, right column), and contrast matches remained close to values observed with the uniform disk. This experiment supports a critical role of the illusory contour for perceptual segmentation of center from surround.

4. Discussion

Retinotopic separation or perceptual segmentation of the center from surround attenuates the perceived modulation depth of stimuli oscillating in color. Retinal center–surround antagonism is unlikely to account for the current results. Some theories suggest that illusory contour formation may begin as early as the retina due to mechanisms of simultaneous contrast (e.g., Ron & Spitzer, 2011), but physiological measurements indicate the first representation of an illusory contour beyond the LGN (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989; von der Heydt,

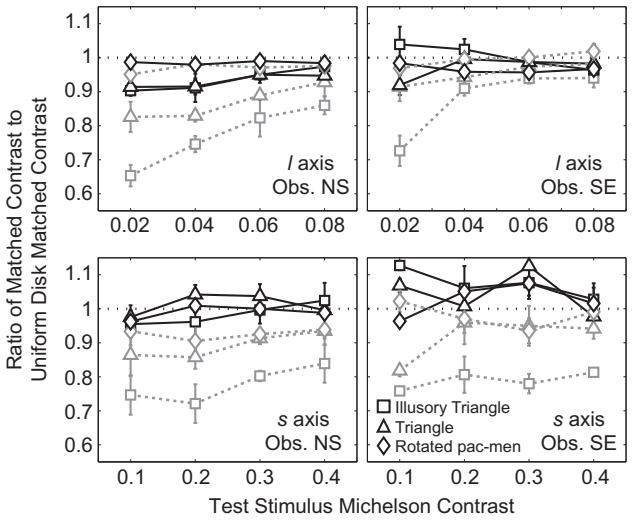

Fig. 6. The ratio of matched contrast to the uniform-disk matched contrast, for luminance-contrast (gray symbols and lines) and equiluminant (black symbols and lines) stimuli for the contours. Stimuli modulating along the *l* and *s* axes are shown in the top and bottom panels, respectively, for observer NS (left column) and SE (right column). Error bars are ±1 SEM of three daily averages.

Peterhans, & Baumgartner, 1984). While previous physiological studies of lateral interactions do not discount a cortical neural representation of contours (e.g., Kozyrev, Silveira, & Kremers, 2007), the current study shows that retinotopic separation is not required to induce changes in the perceived modulation depth of the center. The current results are consistent instead with a cortical neural representation of contours with lateral inhibition following mechanisms sensitive to object segmentation cues.

When contours were from stimuli equiluminant to the test and matching disks, the attenuation of perceived modulation depth was significantly reduced (if not abolished) for both the illusory and physical triangle. This result is in agreement with previous findings that subjective contours are less visible under equiluminant conditions (Gegenfurtner, Brown, & Rieger, 1997; Gregory, 1977; Li & Guo, 1995), so supports the view that the percept of an illusory contour effectively segments center from surround. The difference in attenuation for equiluminant compared to luminance-contrast contours also suggests the segmenting contours are represented in a pathway sensitive to luminance contrast.

Somewhat surprisingly, the illusory triangle consistently showed stronger attenuation of perceived central modulation than the physical triangle. One possible explanation is an increase in perceived brightness within the illusory area due to pac-men presented as a luminance decrement, which may induce perceived desaturation of hue (and therefore more attenuation of perceived contrast). To test this, the strength of attenuation with an illusory contour was compared with chromatic oscillation along the *s* axis using pac-men presented as a luminance increment or decrement. With a luminance increment compared to decrement, the strength of attenuation was reduced. The strength of attenuation was still greater, however, with the luminance increment compared to the physical triangle. A perceived decrease in saturation may explain some attenuation, but it does not account fully for the strength of attenuation with the illusory triangle. This further supports illusory contours as effective perceptual segmentation cues, regardless of the luminance polarity defining the pac-men.

Another possibility for the stronger attenuation with an illusory compared to physical triangle is that observers may adapt to the physical contours, thus reducing their influence on perceived modulation depth. There is some evidence that adaptation to illusory contours also can reduce their visibility (Ramachandran et al., 1994), but whether such adaptation is functionally similar to that from a high-contrast edge is an open question.

This study is in agreement with recent findings illustrating the importance of perceptual organization over spatial retinally defined relations in brightness and color appearance. In the luminance domain, moving a physical contour in depth, so it appears to be in front of the center it segments from a surround (but which, again, does not change the retinotopic separation of center from surround), eliminates the attenuation of perceived brightness modulation found when the contour appears in the same stereoscopic depth plane as the other stimuli (D'Antonia & Shevell, 2007). Color appearance will differ depending also on whether a figure and its ground appear grouped (Schirillo & Shevell, 2000) or segmented into distinct layers (Wollschläger & Anderson, 2009). Experimental results here demonstrate that perceptual segmentation cues also alter perceived temporal oscillations of color.

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